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SLIFERIA, A NEW OVOVIVIPAROUS COCKROACH GENUS (BLATTELLIDAE) AND THE EVOLUTION OF OVOVIVIPARITY IN BLATTARIA (DICTYOPTERA)

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Abstract.—***Sliferia***, a new ovoviviparous blattellid cockroach genus from the Seychelle Islands is described. It includes *Sliferia lineaticollis* (Bolívar) n. comb., and *Sliferia* sp. False ovoviviparity occurs in 1 genus of Pseudophyllodromiinae, 1 genus of Blattellinae (Blattellidae), and practically all subfamilies and genera of Blaberidae. True ovoviviparity is found in 2 blaberid genera of Panesthiinae (Geoscapheini). False viviparity is known only in 1 species of Blaberidae (Diplopterinae). The evolution of ovoviviparity in the Blattaria is discussed.

Key Words: *Sliferia* n. gen., Blattellidae : Pseudophyllodromiinae, ovoviviparity, cockroaches

While studying some of Bolívar's types of cockroaches from the Seychelles, I found that *Blattella lineaticollis* Bolívar is ovoviviparous and belongs in a new genus which I describe here. The specimens were borrowed from the British Museum (Natural History) (BMNH).

Sliferia Roth, NEW GENUS

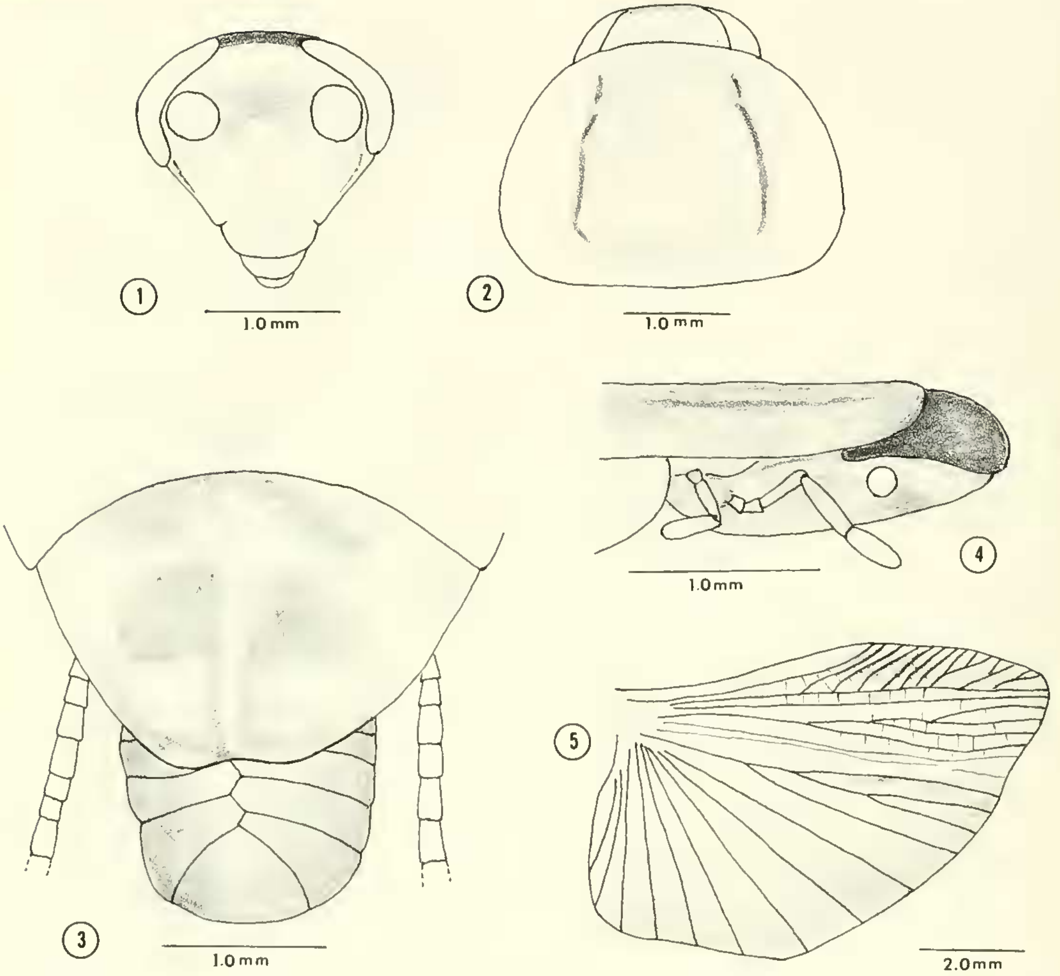
Type species by selection: *Blattella lineaticollis* Bolívar.

Etymology.—The name honors the late Dr. Eleanor H. Slifer (McIver 1987: 195), insect morphologist and colleague.

Description (♀ only; ♂ unknown).—Head triangular (Fig. 1), strongly flattened (Fig. 4). Tegmina and wings fully developed. Tegmina with discoidal vein unbranched, cubitus and median veins and their branches diagonal. Hind wing with discoidal and median veins simple, cubitus vein straight with complete branches, incomplete branches absent, apical triangle small (Fig. 5). Anteroventral margin of front femur with a row of piliform spinules terminating in 2 large spines (Type C_2); pulvilli present on 4 proximal tarsomeres, tarsal claws strongly asymmetrical, unspecialized, arolia present. Ovoviviparous; ootheca, not rotated, is retracted with eggs in original vertical position.

Comments.—Unfortunately, the male is unknown but needed to complete the generic description. The females are similar to *Balta* in front femur armament, tarsal claws, and wing venation. But, they can be distinguished from that genus by the strongly flattened triangular head, reminiscent of the Australian genus *Mediastinia* Hebard (1943: 9).

Only two species are known, the type species and a taxon I did not name because it differed principally only in color from *lineaticollis*. Both are described below.



Figs. 1–5. *Sliferia lineaticollis* (Bolívar). 1–4. Female holotype. 1, Head. 2, Pronotum. 3, Subgenital plate and protruding ootheca (ventral view). 4, Head and part of pronotum (lateral view). 5, Paratype, sex unknown, hind wing.

Sliferia lineaticollis (Bolívar), New Combination

Blattella lineaticollis Bolívar, 1924: 327; Chopard, 1951: 143; Scott, 1933: 340; Princis, 1969: 1007 (sp. incertae sedis); Roth, 1985: 211 (sp. incertae sedis).

Material examined.—Holotype: Female (carrying an ootheca internally), Mahé, 1908-9 Seychelles Exp., Percy Sladen Trust Exped. Brit. Mus., 1926-203 (BMNH).

Paratype.—1 (terminal abdominal segments missing), same data as holotype (BMNH).

Male.—Unknown.

Female.—Interocular space about same as distance between antennal sockets (Fig. 1). Palpal segments 4 and 5 about equal, each longer than segment 3. Tegmina and wings extending beyond end of abdomen. Hind wing with costal veins weakly thickened distad; cubitus vein with 3 complete and no incomplete branches, apical triangle small (Fig. 5). Supraanal plate trigonal, apex weakly indented.

Measurements (mm).—Length, 9.3; pronotum length × width, 2.4 × 3.5; tegmen length, 9.5.

Coloration.—Head with occiput pale, a black transverse band on vertex then a whitish hyaline area and a broad, uneven, brown transverse band between antennal sockets, remainder yellowish brown (Fig. 1). Pronotal disk yellowish brown with narrow dark brown longitudinal lines demarcating it laterally, broad lateral regions hyaline (Fig. 2). Tegmina yellowish brown, hyaline, mediastine vein dark brown. Abdominal terga light yellowish brown with dark infuscation laterally on distal segments; terminal segments blackish brown; supraanal plate blackish with a dirty white transverse stripe basally, a similarly colored macula medially near apex. Abdominal sterna with yellowish brown lateral borders, remainder mottled brownish. Cerci dark brown on proximal segments becoming paler distad.

Ootheca.—The holotype is carrying a fully formed egg case in the upright position (keel region dorsad) inside the abdomen, with a small part of the ootheca protruding beyond the end of the abdomen (Fig. 3). The exposed keel region is flat and lacks raised respiratory serrations. Those eggs seen through the ventral hyaline regions of the oothecal membrane are apparently undeveloped.

Comments.—Scott (1933: 340) and Chopard (1951: 143) found this species in the axils of leaves of screw pines (*Pandanus* sp.) and the palm *Verschaffeltia splendida*.

The holotype was collected probably while she was ovipositing and had not yet retracted the ootheca completely into the brood sac. Or, she may have completed oviposition but partly extruded the egg case when she was killed. Several years ago (Roth 1985: 211) I noted that this female was carrying an ootheca but I incorrectly stated that it was rotated and I failed to point out that it was carried internally.

Sliferia sp.
Figs. 6–8

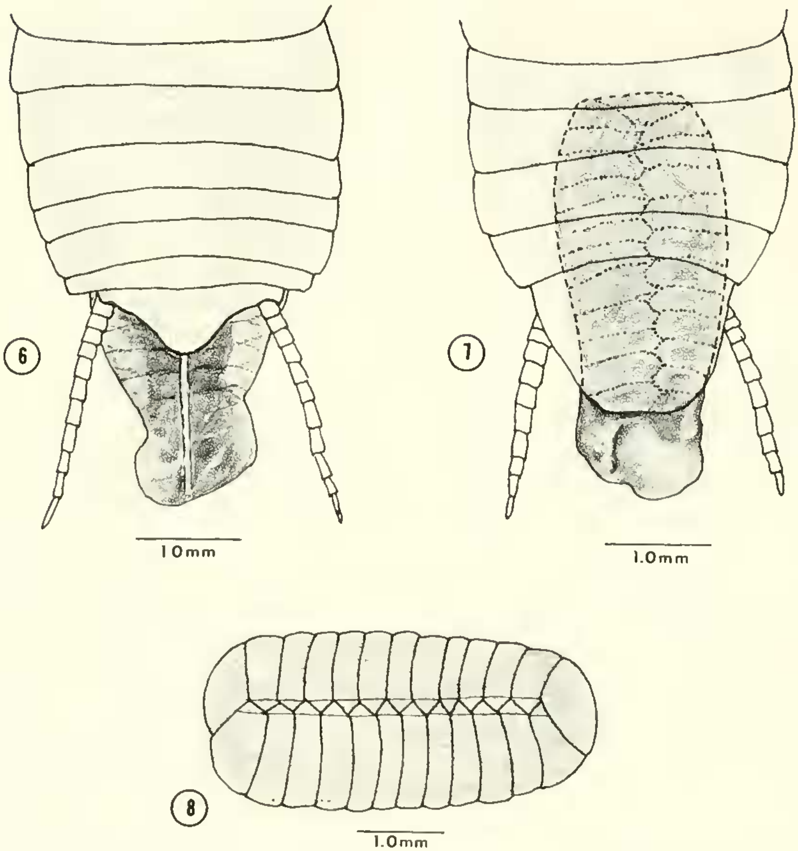
Material examined.—Seychelles, La Digue, 1 ♀ (carrying ootheca internally), 7.III.1953, E. S. Brown, presented by Comm. Inst. Ent. B.M. 1954-368, genitalia slide 264 (BMNH).

Female.—Head exposed, strongly flattened; palpal segments 3 and 4 equal, each slightly larger than segment 5; interocular space less than distance between antennal sockets. Tegmina and wings fully developed (glued together), extending beyond end of abdomen. Front femur Type C_2; pulvilli present on 4 proximal tarsomeres, tarsal claws strongly asymmetrical, unspecialized, arolia present. Supraanal plate trigonal, apex rounded (Fig. 6).

Measurements (mm).—Length, 9.9; pronotum length × width, 2.3 × 3.3; tegmen length, 9.2.

Coloration.—Head with occiput pale, hyaline; edge angular where vertex leads into flattened face, with a narrow, transverse brown line, then a colorless hyaline area and a small, poorly defined, light brown macula, rest of face pale. Pronotal disk yellowish, without markings, broad lateral regions hyaline. Tegmina almost colorless hyaline. Abdominal terga yellowish without dark markings. Abdominal sterna pale, in part hyaline. Cerci with ventral surface darker than dorsal, inner lateral edges of segments narrowly infuscated. Legs pale.

Ootheca.—The female was carrying an ootheca that was partially collapsed and protruding from the end of the abdomen. Most of the egg case could be seen through the hyaline parts of the abdominal sterna and it occupied a large part of the abdominal cavity (Figs. 6, 7). The ootheca was oriented with its keel region dorsad and was not rotated prior to being retracted into the brood sac. I placed the abdomen in 10% KOH for



Figs. 6–8. *Sliferia* sp., pregnant female from La Digue, Seychelles. 6, Abdomen (dorsal view). 7, Abdomen (ventral view; most of the internal ootheca is visible through the abdominal sterna). 8. Ootheca removed from abdomen and treated with KOH (dorsal view).

several minutes and the egg case floated out of the abdomen and swelled (Fig. 8). It was 4.5 mm long, wider than high, and contained 25 eggs, some of which showed early embryonic development. The oothecal membrane was thin, flexible, and completely covered the eggs. There were neither serrations (respiratory tubules) in the keel region, nor calcium oxalate crystals.

Evolution of ovoviviparity and viviparity in the Blattaria

In the two phyletic lines of Blattaria, ovoviviparity and viviparity arose in the superfamily Blaberoidea but not in the Blattoidea. It was originally believed that ovoviviparity was found only in the Blaberidae (McKittrick 1964, Roth 1970). Recently it was discovered in an African genus *Stayella* Roth (Roth 1982a, 1984) (Blattellidae: Blattellinae), and now in *Sliferia* (Blattellidae: Pseudophyllodromiinae of Vickery and Kevan 1983: 157 = Plectopterinae of McKittrick 1964). Internal incubation of eggs by Blattaria evolved from oviparous ancestors (Fig. 9) and required changes in physiology, morphology, and oviposition behavior. The families and subfamilies shown in Fig. 9 are principally those of McKittrick (1964) except for the Nocticolidae and Attaphilinae which she did not study. I (Roth 1988: 300) discussed the

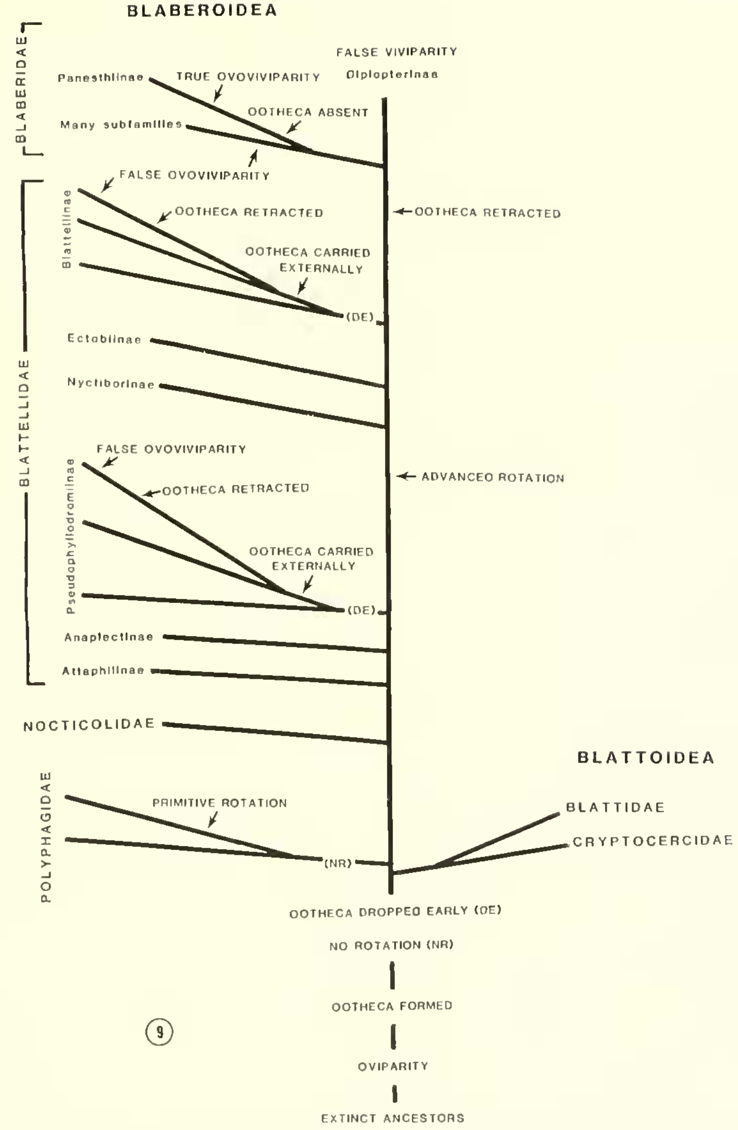


Fig. 9. Possible evolution of ovoviviparity and viviparity in the Blattaria.

taxonomic position of the former family and McKittrick (*in* Roth 1968c: 135) placed the Attaphilinae in the Blattellidae.

Extinct ancestors.—Vishniakova (1968) summarized the literature on fossil cockroaches. The oviparous females had external ovipositors and have been found in the Upper Carboniferous and Permian deposits of Europe, Asia, and North America, and in the Triassic and Jurassic deposits of the USSR. Presumably the species laid eggs singly in plants or soil. With time, the ovipositor was gradually reduced in length. Eventually a structure evolved hidden within the vestibulum that was used to form an ootheca containing a group of eggs. In some Jurassic species, the ovipositor is very short and the transition from long external ovipositors to short internal ones apparently took place towards the end of the Mesozoic.

Oothecae have been described from the Carboniferous, but the fossils only remotely resemble an egg case (Roth 1967b: Fig. 16), and most likely are imprints or fragments of other organisms (Brown 1957, Vishniakova 1968). An ootheca from the Eocene (Brown 1957, Roth 1967b: Fig. 15) appears to be an authentic blattellid egg case. McKittrick (1964) suggested that the primitive cockroach ootheca was probably a packet of eggs glued together like the ootheca of the termite *Mastotermes darwiniensis* Froggart (Roth 1967b: Fig. 17). Except for two genera (possibly four) of ovoviviparous Panesthiinae, cockroaches that have been studied produce an ootheca.

Selection pressure.—According to Vishniakova (1968) the selection pressure for the reduction of the external ovipositor and the change from oviparity to internal incubation of the eggs was the appearance in the Carboniferous to the Jurassic of predators and parasites that destroyed eggs. A number of Hymenoptera are known that destroy cockroach eggs (Roth and Willis 1960: 234–255). Some wasps can oviposit through a deposited and hardened ootheca. For example *Tetrastichus hagenowii* (Ratzeburg) lays eggs in oothecae of *Periplaneta americana* (Roth and Willis 1954b: Plate I). Other wasps can oviposit into the soft ootheca before the wall hardens. For example, *Evania appendigaster* (Linn.) lays eggs in the ootheca of *P. americana* (Kieffer 1912); *Zeuxevania splendidula* Costa into the oothecae of *Loboptera decipiens* (Germar) (Genieys 1924). *Anastatus floridanus* Roth and Willis oviposits through the soft walls of the egg case of *Eurycotis floridana* (Walker) while the ootheca is still carried by the female and before it hardens and is deposited (Roth and Willis 1954c: Fig. 9); the female often buries the ootheca in sand and once this is done the wasp usually can't locate it for oviposition. Oothecae still attached to females of *Blattella dethieri* Roth and *Blattella armata* (Princis) have contained a single evaniid wasp (Roth 1985: Figs. 92C, 102D, 102E). Schletterer (1889) found the evaniid *Brachygaster minutus* (Olivier) in the ootheca of *Blattella germanica* (Linn.). Wasps that parasitize the eggs of *Blattella* oviposit into the ootheca while it is carried by the female. The cockroach continues to carry the egg case while the eggs are being eaten by the parasitoid.

In classifying the placement of parasitic wasp eggs in relation to host species, Clausen (1972) erected the category: Egg placed in the embryo while the latter is still within the parent. Although this behavior was not known to occur, Clausen believed that it probably could occur. *Evania appendigaster* was claimed to parasitize the eggs of the blaberid *Leucophaea maderae* (Fab.) (Schletterer 1889, Bordage 1896, Kieffer 1912). But after realizing that *Leucophaea* is ovoviviparous, Bordage (1913) admitted misidentifying the parasitized ootheca and concluded that the developing eggs of *Leucophaea* are protected against egg parasites because they are carried within the female. Sells (1842) reported that an ootheca of *Leucophaea maderae* (= *Blaberus maderae*) contained ninety six specimens of a small chalcid wasp; some oothecae had a round hole through the side of the capsule from which the wasps had emerged. Sells statement that the ootheca had a keel with 16 dentations indicates that the parasitized oothecae probably were *Periplaneta americana* (Roth and Willis 1954b: Plate III).

It is true that eggs of ovoviviparous cockroaches have not been found to be parasitized by wasps. The oviposition of some wasps into an ootheca while it is still carried by the female is evidence that wasps that destroy the eggs of ovoviviparous species probably will be found. I suspect that wasp parasitoids will be found in species of *Stayella* with oothecae similar to those of *Blattella* but incubated internally. The *Stayella* ootheca could be parasitized as it is being formed and before it is retracted into the brood sac. If the female cockroach extruded the parasitized ootheca when the wasp matured, the adult parasite could easily escape the host abdomen. Similarly, the eggs of ovoviviparous Blaberidae could be parasitized while the ootheca was being formed before it was retracted into the uterus. Protection from wasp egg parasitoids could probably be assured if the eggs were never exposed to the outside, and this occurs only in true ovoviviparous genera *Macropanesthia* and *Geoscapheus.*

Laurentiaux (1951) suggested that the ootheca appeared as an adaptive response to climatic and hygrometric changes. The oothecal membrane in the Blattoidea is capable of preventing desiccation of the eggs even when exposed to very low humidities. In the Blattellidae, the protective covering varies in its ability to prevent water loss, and in the Blaberidae, the greatly reduced covering does not prevent the eggs from losing water even in very high humidities. These studies in water loss (Roth and Willis 1955b, Roth 1967b) indicate that an important selection pressure for the evolution of internal incubation was the prevention of egg death from water loss.

Ootheca formation.—Roth (1974) found that there has been a divergence of the centers that control oviposition in the Blaberoidea and Blattoidea. The brain is not needed for oviposition in the Blaberidae where the control center for formation, 90° rotation, and retraction of the ootheca into the brood sac probably lies in the last abdominal ganglion. In the Blattidae the brain is needed to initiate egg case formation, but it is unnecessary once the process has begun.

During oviposition, the female extrudes some colleterial gland secretion as a soft rubbery blob in a mold formed by the intersternal membrane of the vestibulum. As the eggs leave the gonopore they are guided by the ovipositor valves into the blob of secretion where, with micropylar ends dorsad, they line up, alternating sides, and protrude from the end of the abdomen as a double row (Roth and Willis 1954a: Pl. 5). In oviparous species the newly formed ootheca is pale and soft but hardens quickly when exposed to air. The dorsal ovipositor valves serve as a mold and impart characteristic shapes to the keel. Each egg lies in a cell surrounded by an air space connected to a duct in the keel that leads to external air. Oothecae of different species differ in size, shape, surface texture, keel serration, and the number of contained eggs (Roth, 1968b, 1971). Ovoviviparous species of Blaberidae and species of Blattellidae that carry their oothecae externally during embryogenesis generally have a larger number of eggs per ootheca but produce fewer oothecae than oviparous species that drop their egg cases shortly after forming them (Roth 1970: fig. 21).

The paired ovaries of cockroaches consist of a variable number of ovarioles. Each ovariole consists of a variable number of oocytes and at oviposition supplies one yolk-filled egg in the ootheca. Those oocytes containing yolk at oviposition are found in a region known as Zone V. Both the Blattoidea and Blaberoidea probably evolved from taxa in which three or more oocytes contained yolk in Zone V. In the Blaberoidea there is an evolutionary trend towards a decrease in the number of oocytes in Zone V, as well as the total number of oocytes per ovariole. The Polyphagidae have two or three oocytes in Zone V, and a large number of oocytes per ovariole. Species of Blattellidae have one or two oocytes in Zone V, and show some reduction in total number of oocytes. In ovoviviparous and viviparous Blaberidae there is a marked reduction in the number of oocytes, and only one oocyte develops yolk at oviposition. Species like *Blattella* that carry their oothecae externally during embryogenesis have only one oocyte in Zone V and few oocytes per ovariole as in most Blaberidae (Roth 1968c).

During pregnancy in ovoviviparous and viviparous taxa, the corpora allata are inhibited and yolk deposition does not occur in the oocytes as long as there is an ootheca in the uterus. Yolk inhibition also occurs in pregnant *Blattella*. In ovoviviparous taxa the colleterial glands show cyclical activity corresponding to the ovarian cycle: active during the preoviposition period, inactive during gestation, and active again after parturition (Roth 1968b). In oviparous species that drop their oothecae early, the colleterial glands secrete protein continuously, there is no distinct cycle related to oviposition, and during the height of their reproductive period females produce oothecae frequently.

In oviparous species, a hardened ootheca is carried externally for various lengths of time. It can be deposited shortly after its formation or retained for the full gestation period (Roth and Willis 1958: figs. 1–12, 30–37). When first deposited the eggs may have sufficient water and yolk to complete development (Blattidae), or they have sufficient yolk but require water which is obtained from the female (*Blattella* spp., *Lophoblatta* spp.) or from the substrate (most Blaberoidea, except Blaberidae) (Roth 1967b, 1968a, Roth and Willis 1955b).

Once the ootheca is formed, the female may oviposit in one of the following ways:

No rotation, ootheca dropped early (NR).—The original vertical position of the ootheca is not changed and the egg case is deposited shortly after its formation (Roth and Willis 1954a: Pl. 5). The female may try to hide the dropped egg case by burying it or covering it with a mixture of saliva and chewed substrate, and then she abdandons it (McKittrick 1964). Examples are Nocticolidae (Chopard 1932: 489), some species of Polyphagidae, Blattellidae (Attaphilinae, Anaplectinae, many genera of Pseudophyllodromiinae), all species of Blattidae and Cryptocercidae (Roth 1968b).

Ootheca carried externally during gestation.—These oviparous species carry their oothecae attached to the end of the abdomen until the eggs hatch. The ootheca can be held in the original vertical position as in *Lophoblatta* (Roth 1968a) or rotated 90° as in *Blattella* (Roth and Willis 1958: Pl. 25, figs. 7–12, Pl. 27, figs. 29–37).

Primitive rotation.—The ootheca is rotated 90° and deposited shortly after its formation. The egg case has a flange which is held by the paraprocts and none of the anterior eggs are held within the vestibulum in contact with the tissues of the female (Roth 1970: fig. 5). Primitive rotation is known only in some Polyphagidae, including *Arenivaga* (*Arenivaga*) spp. (Roth 1967a) and *Latindia* sp. (Roth 1971: 128).

Advanced rotation.—After the ootheca is formed and still attached, it is rotated 90° so the keel is lateral, to the left in Blaberidae, and the right in most Blattellidae. Several of the most anterior eggs, those leaving the oviduct last, are in contact with the vestibular tissues of the female. This contact is necessary for oviparous species like *Blattella* spp. and *Lophoblatta* spp. whose eggs obtain water from the mother during embryogenesis (Roth 1967a). Examples are Nyctiborinae, Ectobiinae, most Blattellinae and Pseuphyllodromiinae, and all Blaberidae that form an ootheca.

Oothecal changes.—During the evolution of ovoviviparity in the Blattellidae, changes in the ootheca involved reduction in height of the keel and finally loss of the keel, and softening of the increasingly flexible protective membrane due to the gradual reduction and finally loss of calcium oxalate crystals. The oothecal changes in the Blaberidae were greater than those that took place in the Blattellidae (*Blattella, Stayella, Sliferia*). In some blaberids the oothecal wall is relatively thick and covers the eggs completely. In others, the wall shows various degrees of reduction and does not cover the micropylar ends of the eggs. Although the keel is absent in most blaberids, relicts of this structure occur in *Epilampra cribrosa* Burmeister (Roth 1968b), for example.

Ootheca retracted.—After the ootheca is formed, it is retracted into the brood sac with or without being first rotated 90° (Roth and Willis 1954a: figs. 74–79, 86–90).

McKittrick (1964: 116) believed that rotation of the ootheca freed the keel from the ovipositor valve bases, which supposedly block anterior movement of the vertical ootheca. But, as noted above, in the Blaberidae the ootheca is reduced, keel serrations are absent or rarely subobsolete so rotation is not necessary to free its keel from the valve bases (Roth 1967a). In the blattellid *Sliferia* the ootheca lacks keel serrations and is retracted in the vertical position.

In the ovoviviparous Blaberidae, the eggs enlarge in the brood sac during embryogenesis (Roth and Willis: 1955b, fig. 7A–D). When stretched by a newly deposited ootheca, the blaberid uterus presses against the inner surfaces of the terga and sterna and leaves room laterally for expansion (Roth 1967a: 85). Just before parturition the ootheca occupies practically the entire abdomen (Roth 1967a: 85). But even at this time it is difficult to determine if the female is pregnant because the abdomen hasn't stretched as much as it would have had the ootheca been retracted into the uterus in the vertical position. To determine pregnancy one has to separate the supraanal and subgenital plates and look for the terminal end of the ootheca. Cockroaches generally are relatively flat insects and tend to hide in narrow crevices and spaces where they can escape from predators. It is advantageous for the eggs to be so oriented in the uterus that their increase in size does not markedly increase the height of the abdomen. In *Blattella* rotating the ootheca allows the insect to hide in narrower crevices than would be possible if the ootheca was carried externally in the vertical position. Wille (1920) measured the minimum gaps within which various stages of *B. germanica* could move. Gravid females 1 day before oviposition needed a space of 4.5 mm; with the ootheca in the vertical position, the width decreased to 3.3 mm, and after the egg case was rotated the female could move in a space 2.9 mm high. In *Sliferia*, the eggs probably do not increase much in length during embryogenesis and because its ootheca is wider than high rather than higher than wide, rotation is not necessarily advantageous and the ootheca is retracted in the vertical position.

False ovoviviparity.—The ootheca is formed and retracted into the brood sac. Initially the eggs have enough yolk to complete development but must obtain water from the female during embryogenesis. The marked similarity of the oothecae of *Stayella* and *Blattella* (Blattellinae), and *Sliferia* and *Lophoblatta* (Pseudophyllodromiinae), strongly suggests that the ancestors of the two ovoviviparous genera were *Blattella*-like and *Lophoblatta*-like species in their respective subfamilies. Cockroaches with false ovoviviparity include two genera in the Blattellidae, and all Blaberidae except two truly ovoviviparous genera, and one viviparous species.

True ovoviviparity.—No ootheca is formed. During oviposition the eggs are never exposed to the outside but pass directly into the vestibulum and brood sac where they lie in a jumbled mass. At oviposition the eggs have enough yolk to complete development, and take up only water from the mother during embryogenesis (Rugg and Rose 1984a). Examples include *Macropanesthia rhinoceros* Saussure, *Geoscapheus dilatatus* (Saussure), and probably species of *Neogeoscapheus* and *Parapanesthia*. All four of these genera were originally placed in the Panesthiinae, tribe Geoscapheini (Roth 1982b), but because of the absence of an ootheca Rugg and Rose (1984b) placed them in the family Geoscapheinae.

Roth (1968b: 103) speculated that complete loss of the oothecal membrane would result in eggs being simply glued together in a double row, presumably like the ootheca of *Mastotermes darwiniensis*, and then could be retracted into the brood sac. Rugg and Rose's discovery shows that some species can deposit their eggs in the uterus without first extruding them in a double row.

False viviparity.—The ootheca is very small, containing about a dozen eggs, and has an incomplete covering membrane (Roth and Hahn 1964). Because of their small size, hardly any of the eggs are seen during oviposition, but the ootheca is rotated and retracted into the brood sac. Initially the eggs lack sufficient yolk and water to complete development (Roth and Willis 1955a). During embryogenesis the embryos drink water and dissolved proteins and carbohydrates, synthesized and transported by the brood sac (Stay and Coop 1973, 1974, Ingram et al. 1977). *Diploptera punctata* (Eschscholtz) is the only known example, although other species in the genus probably have the same type of reproduction.

True viviparity.—No example in cockroaches is known. In true viviparity, the eggs would pass directly into the brood sac without first being exposed externally, and they would obtain solids and water from the female during embryogenesis.

The discovery that ovoviviparity occurs in two subfamilies of Blattellidae rather than only in the Blaberidae as proposed by McKittrick (1964) does not contradict her basic thesis that ovoviviparity arose only in the Blaberoidea and not in the Blattoidea. In this regard there is no reason to revise McKittrick's system.

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